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Published in:
Canadian Journal of Fisheries and Aquatic Sciences

Link to article, DOI:
10.1139/cjfas-2015-0098

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

NRC Research Press

ARTICLE

Maximizing fisheries yields while maintaining community structure[1]

Jeppe Kolding, Nis S. Jacobsen, Ken H. Andersen, and Paul A.M. van Zwieten

Abstract: Under the ecosystem approach to fisheries, an optimal fishing pattern is one that gives the highest possible yield while having the least structural impact on the community. Unregulated, open-access African inland fisheries have been observed to sustain high catches by harvesting a broad spectrum of species and sizes, often in conflict with current management regulations in terms of mesh and gear regulations. Using a size- and trait-based model, we explore whether such exploitation patterns are commensurable with the ecosystem approach to fisheries by comparing the impacts on size spectrum slope and yield with the different size limit regimes employed in the Zambian and Zimbabwean sides of man-made Lake Kariba. Long-term multispecies data under fished and unfished conditions are used to compare and validate the model results. Both model and observations show that the highest yields and low structural impact on the ecosystem are obtained by targeting small individuals in the community. These results call for a re-evaluation of the size-based management regulations that are ubiquitous in most fisheries.

Résumé : Dans l'approche écosystémique des pêches, un régime d'exploitation optimal est celui qui donne le meilleur rendement possible tout en ayant le plus faible impact structural sur la communauté. Il a été observé que des pêches continentales africaines non réglementées et d'accès libre supportent de fortes prises à l'exploitation d'un vaste spectre d'espèces et de tailles, souvent en contravention avec les règlements de gestion en vigueur concernant la taille des mailles et les engins. En utilisant un modèle basé sur les tailles et des caractéristiques biologiques, nous examinons dans quelle mesure de tels régimes d'exploitation sont compatibles avec une approche écosystémique des pêches, en comparant les impacts sur la pente des spectres de tailles et sur le rendement des différents régimes de limites de taille employés sur les côtes zambiennes et zimbabwéennes du lac de barrage Kariba. Des données multi-specifiques de longue durée collectées dans les conditions d'exploitation et de non-exploitation sont utilisées pour comparer et valider les résultats du modèle. Le modèle et les observations montrent tous deux que les rendements les plus élevés et un faible impact structural sur l'écosystème sont obtenus en ciblant les petits individus de la communauté. Ces résultats soulignent la nécessité de réévaluer les règlementations de gestion bases sur les tailles, très répandus dans la plupart des pêcheries.

Introduction

Size selectivity is deeply rooted in fisheries theory and it has been a long-standing policy in fisheries management to protect the juveniles and target the adults (Caddy 1999; Kolding and van Zwieten 2011). These regulations are justified by the results of the traditional yield-per-recruit models (Beverton and Holt 1957) that are widely used for simulations to optimize relative yields as a function of entry age and fishing pressure in single-species assessments. The notion of growth overfishing by harvesting juvenile fish is a result of these models and has become a universally accepted truism for promoting targeting adults only. That so-called nonselective fisheries or indiscriminate fisheries are destructive and depleting stocks is so paradigmatic that it usually does not warrant any verification. Yet, there is increasing evidence that the selective removal of adult fish causes adverse consequences and does not achieve the global official goal of maximizing sustainable yields (United Nations Convention on the Law of the Sea (UNCLOS) 1982; World Summit of Sustainable Development (WSSD) 2002) but instead causes destabilizing changes in the structure of exploited populations and communities (Pope 1991; Anderson et al. 2008; Hsieh et al. 2010; Zhou et al. 2010; Garcia et al. 2012; Law et al. 2012, 2014).

However, maximizing yields is not the only global goal for fisheries management. The main objective of the internationally agreed Convention of Biological Diversity (CBD 1992) is to develop strategies for the conservation and sustainable use of biological diversity in an equitable way, and the so-called "ecosystem approach" is the primary framework for reaching these objectives (United Nations Environment Programme (UNEP) 2000). A priority target of the ecosystem approach is to maintain ecosystem services while conserving the ecosystem structure and functioning (Malawi principle 5). The rationale is that ecosystem function and resilience depends on a dynamic relationship within species, between species and their abiotic environment, so that the conservation of these interactions and processes is of greater significance for the long-term maintenance of biological diversity than simple protection of species (UNEP Conference of the Parties to the Convention on Biological Diversity (UNEP/CBD/COP) (1998).

Received 18 February 2015. Accepted 11 September 2015.

Paper handled by Associate Editor Henrique Giacomini.

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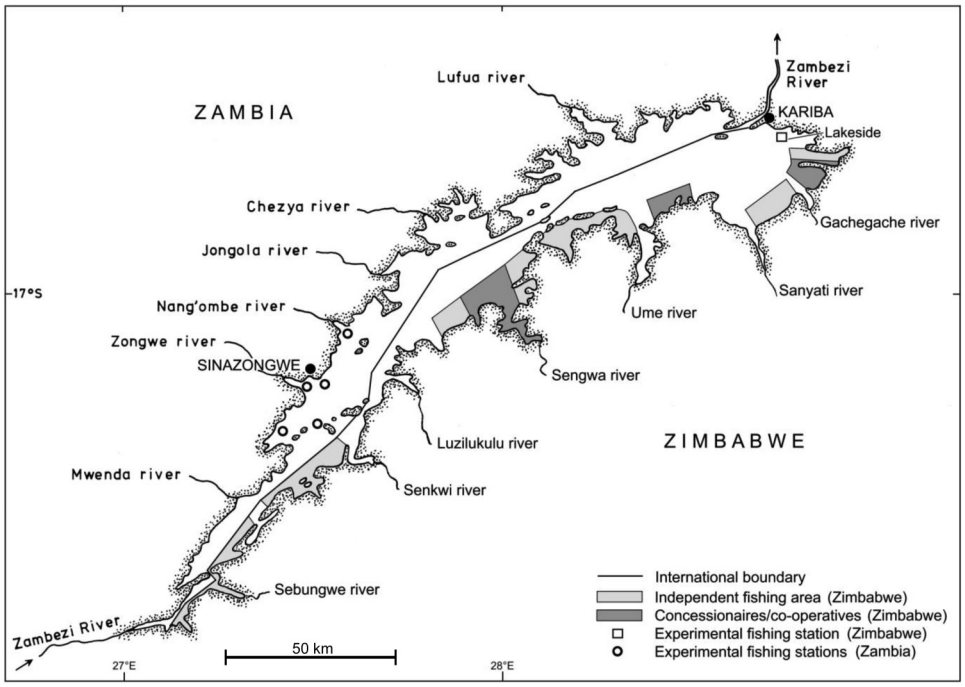
[1]This article is part of a special issue entitled "Size-based approaches in aquatic ecology and fisheries science: a symposium in honour of Rob Peters".

Fig. 1. Map of Lake Kariba on the Zambezi River between Zambia and Zimbabwe. Designated fishing areas in Zimbabwe are indicated, with the rest being protected, while the whole Zambian side is open to fishing. Experimental fishing stations are shown in Zambia around Sinazongwe (open circles) and from the protected nonfished Lakeside area in Zimbabwe near Kariba town (open square). Modified from Kolding et al. 2003*a*.



Thus one of the cardinal questions in the use of renewable biological resources for an expanding human population is how we maximize food production while making the least structural and functional disturbances to ecosystems.

To mitigate many of the adverse ecological effects of selective fishing while supporting sustainable fisheries, it has been suggested to adopt a balanced harvesting strategy that distributes moderate fishing pressure across the widest possible range of species, stocks, and sizes of an ecosystem, in proportion to their natural productivity (Garcia et al. 2012). Such a strategy would prescribe a higher fishing mortality on small fast-growing individuals and species than on larger slow-growing individuals. Although there are several studies that theoretically support this strategy (Law et al. 2012, 2014, 2015; Jacobsen et al. 2014), there are few empirical examples to serve as evidence. One exception is the fishing pattern observed in several high-yielding small-scale inland fisheries in Africa, where the relative proportion of the components in the fish community has been largely maintained by a balanced reduction of all species and size groups (Misund et al. 2002; Kolding et al. 2003*a*, 2003*b*; Kolding and van Zwieten 2011, 2014). This less selective fishing pattern is achieved by combining a large range of different mesh sizes and gear types, often with a strong focus on small species and sizes (Kolding et al. 2015*a*) as they are the most productive and return the highest relative catch per unit effort for the individual fisher. However, such a fishing pattern, which typically involves "indiscriminate" fishing methods, is under current management paradigms considered unethical, destructive, and often technically illegal, and as a consequence, there are often strong conflicts within and between fishers and managers, even under co-management situations (Kolding et al. 2014). Actually, artisanal inland fisheries are considered the least successfully managed fisheries in a recent global meta-analysis (Gutiérrez et al. 2011).

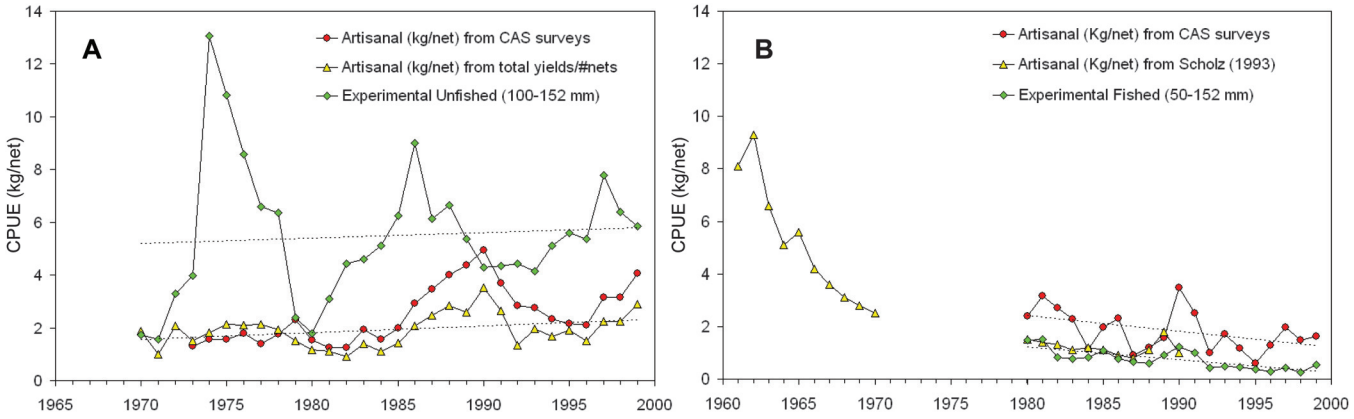
The aim of this paper is to examine the consequences of selective and less selective fishing patterns in terms of total yield and community structure. We use the case of man-made Lake Kariba (Fig. 1), which for historic and political reasons has experienced very different management regimes on its two shores (Zimbabwe on the southern shore and Zambia on the northern shore) (Kolding et al. 2003*a*): although Zimbabwe successfully enforced gear regulations and effort control until recently, the Zambian side can be considered an open-access fishery with no enforcement of technical regulations. We therefore have an example in which one-half of the same ecosystem is managed by enforcing a selective fishing pattern (Zimbabwe) and the other half employs a less selective fishing pattern (Zambia). We apply a recent trait- and size-based multispecies model of the fish community (Andersen and Pedersen 2010), which is particularly suited to make an impact assessment of size-selective fisheries in diverse communities (Andersen and Rice 2010) as it specifically accounts for individual energy budgets and thus captures the indirect effects of the change in community structure that a fishery might cause. The model is calibrated to the fishing pattern, effort, and community structure observed on the two shores of Lake Kariba. We use the model to calculate the yield and community structure under different fishing patterns and levels of fishing mortality. The results confirm the observations that high fishing mortality on small and juvenile fish can give high yields with limited changes to the community structure.

Methods

Lake Kariba

The data are from Lake Kariba (5300 km^2), on the Zambezi River in southern Africa, which is the world's largest man-made reservoir by volume (180 km^3) and is approximately equally shared between Zambia on the northern bank and Zimbabwe on the southern bank (Fig. 1). The Zambezi River provides about 80% of the water inflow, and there is a natural limnological gradient in the lake ecosystem from riverine characteristics in the shallow effluent east that gradually change into a more lacustrine environment near the 120 m dam wall to the west. The gradient in the lake is also reflected in the fish communities, which are dominated by potamodromous species in the eastern basin (Cyprinidae and Distichodontidae) and more sedentary cichlids in the western

Fig. 2. Catch per unit effort time series in the Lake Kariba inshore demersal fishery. (A) Zimbabwe: artisanal mean annual kilograms per net from catch assessment surveys (CAS; circles), total annual yield / total number of nets (triangles, trend not significant), and mean annual experimental kilograms per 45 m net set (diamonds, trend not significant) in the mesh range 100–152 mm (comparable with artisanal mesh range) from an unfished area. (B) Zambia: artisanal mean annual kilograms per net from CAS surveys (circles, trend not significant), mean annual kilograms per net from Scholtz (1993) (triangles), and mean annual experimental kilograms per 45 m net set (diamonds, trend significant, $p < 0.01$) in the mesh range 50–152 mm (comparable with artisanal mesh range) from the fished area. Redrawn from Kolding et al. (2003*a*). (Available in colour online.)



basin (Begg 1974). For cultural and political reasons, the two sides of the lake have been exposed to very different management regimes, which in retrospect can be considered a grand-scale ecological experiment (Kolding et al. 2003*a*). While the Zimbabwean side has been strictly managed and controlled in terms of licensed fishers, restricted fishing grounds, and minimum mesh-size regulations, the Zambian side has virtually been an open-access fishery with no enforcement of regulations since its independence in 1964. The result has been two very different scenarios of development of the inshore stocks (Fig. 2), which can be considered homologous but mutually independent as very few of the demersal, originally riverine, species venture across the deep pelagic zone created by the lake (Ngalande 1995; Kolding et al. 2003*a*). Actually, the pelagic middle of the lake was uninhabited by fish until the introduction of the Tanganyika clupeid (*Limnothrissa miodon* or kapenta) in 1967–1968 to fill this vacant niche. Presently, the kapenta fishery is the largest on the lake, yielding about 30 000 metric tons (t) per year, and has virtually no bycatch of the inshore species (Nyikahadzoi and Råkjær 2014). Although the overall fish biomass has been fluctuating due to environmental climate-driven variation (Karenge and Kolding 1995*a*, 1995*b*), the long-term trend (measured as standardized catch per unit effort, CPUE) in the Zimbabwe inshore fishery is stable (Fig. 2A), whereas it has declined exponentially in Zambia (Fig. 2B) in accordance with the usual expectations of increased effort. The total number of recorded nets over the period under investigation (1980–1994) is about seven times higher in Zambia than in Zimbabwe, and the corresponding average annual yield is approximately 6000 t in Zambia versus 1200 t in Zimbabwe (Kolding et al. 2003*a*). The average catch rates of the fishers (kg per 50 m net) are about 2.7 in Zimbabwe compared with 2.0 in Zambia (Fig. 2). The relatively small difference in catch rates despite the large differences in effort and biomass is obtained by the Zambian fishers using a suite of smaller mesh sizes starting from around 2 inches (50 mm), whereas the Zimbabwean fishers are obeying the minimum legal mesh size of 4 inches (102 mm) stretched mesh and above (Fig. 3).

Experimental fishing from the respective management institutions on each side (Department of Fisheries in Zambia and Department of Natural Park and Wildlife Services in Zimbabwe) has been performed regularly over the whole period (*i*) in a protected area with no other fishing near the town of Kariba in Zimbabwe and (*ii*) on the fishing grounds close to Sinazongwe in Zambia from 1980 and onwards (Fig. 1). These data are described in detail in Karenge (1992), Musando (1996), and Songore (2002) and summarized in Kolding et al. (2003*a*). The experimental fishing consists of standardized multifilament gillnet fleets with 13 mesh sizes ranging from 1 to 7 inches in half-inch (13 mm) steps. All fish from the experimental fishing are recorded by length, weight, sex, gonadal stage, and mesh size in which they were caught. The experimental fish data, covering the period 1980–1994 when the sampling design was homogenous and standardized on both sides of the lake, consists of nearly 75 000 fish from 1059 samples from the unfished area in Zimbabwe and close to 50 000 fish from 958 samples from the fished area in Zambia. Both data sets are trimmed to cover the nine mesh sizes (13 mm increments) in the 50–152 mm range to correspond with the artisanal fishery. Thus, in summary, we have four separate time series of information (Fig. 2): artisanal catch and effort from two different and separate management regimes in the same lake and experimental catch and effort with individual-species demographic data from an unfished area (serving as baseline) and a heavily fished area. The fish species diversity has gradually increased in the lake since its creation (Kolding and Songore 2003), with no significant differences between the two sides (Musando 1996; Kolding et al. 2003*a*), and the species composition in both the experimental fishery (Fig. 4) and the artisanal fishery (Fig. 5) is practically identical on both sides along the gradient, albeit the Zambian fishery contains a higher proportion of small species due to the use of smaller mesh sizes. Thus the only significant difference between the two sides of the lake is the standing fish density and total landings.

Size-based model

The model is size- and trait-based and calculates the number distribution of fish as a function of their size (w) and their maximum asymptotic size (W_∞) as $N(w, W_\infty)$. The model is based on a few ecological assumptions, which are formalized in a set of mathematical equations (Table 1). The general model is described in detail in Hartvig et al. (2011), and the specific setup used here is described in Jacobsen et al. (2014) with a set of parameters calibrated to Lake Kariba (Table 2). Assumptions are made only at the level of the individuals in terms of their physiology, their encounter with prey, and their reproductive capability. The central assumption is that big individuals eat smaller individuals with a log-normal size preference (Ursin 1973; Table 1, eq. M1). The size preference is used to determine the amount of food that an individual encounters, which depends on a search rate that scales

Fig. 3. Observed artisanal fishing pattern in Lake Kariba (Zambia (open bars) and Zimbabwe (hatched bars)) as relative distribution of recorded mesh sizes in the 1980–1994 catch assessment surveys (Zambia) and a 1993 frame survey (Zimbabwe). Data from Department of Fisheries (Zambia) and Department of National Parks and Wildlife (Zimbabwe).

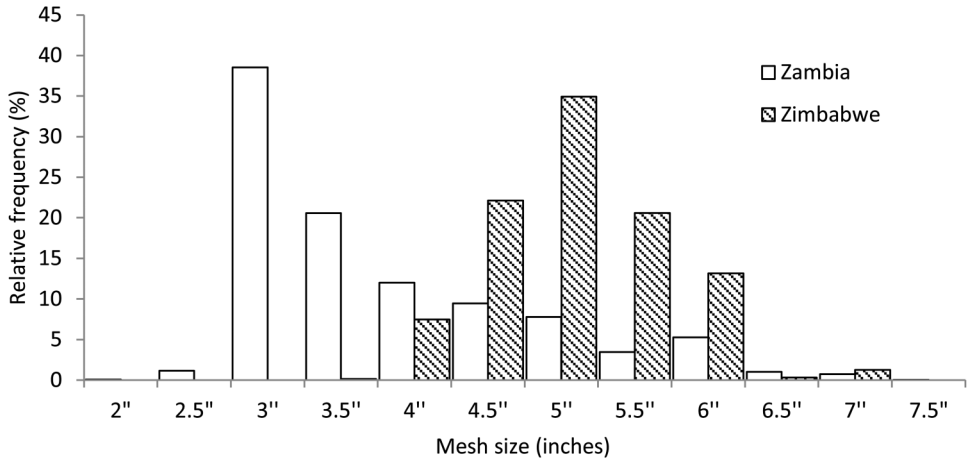
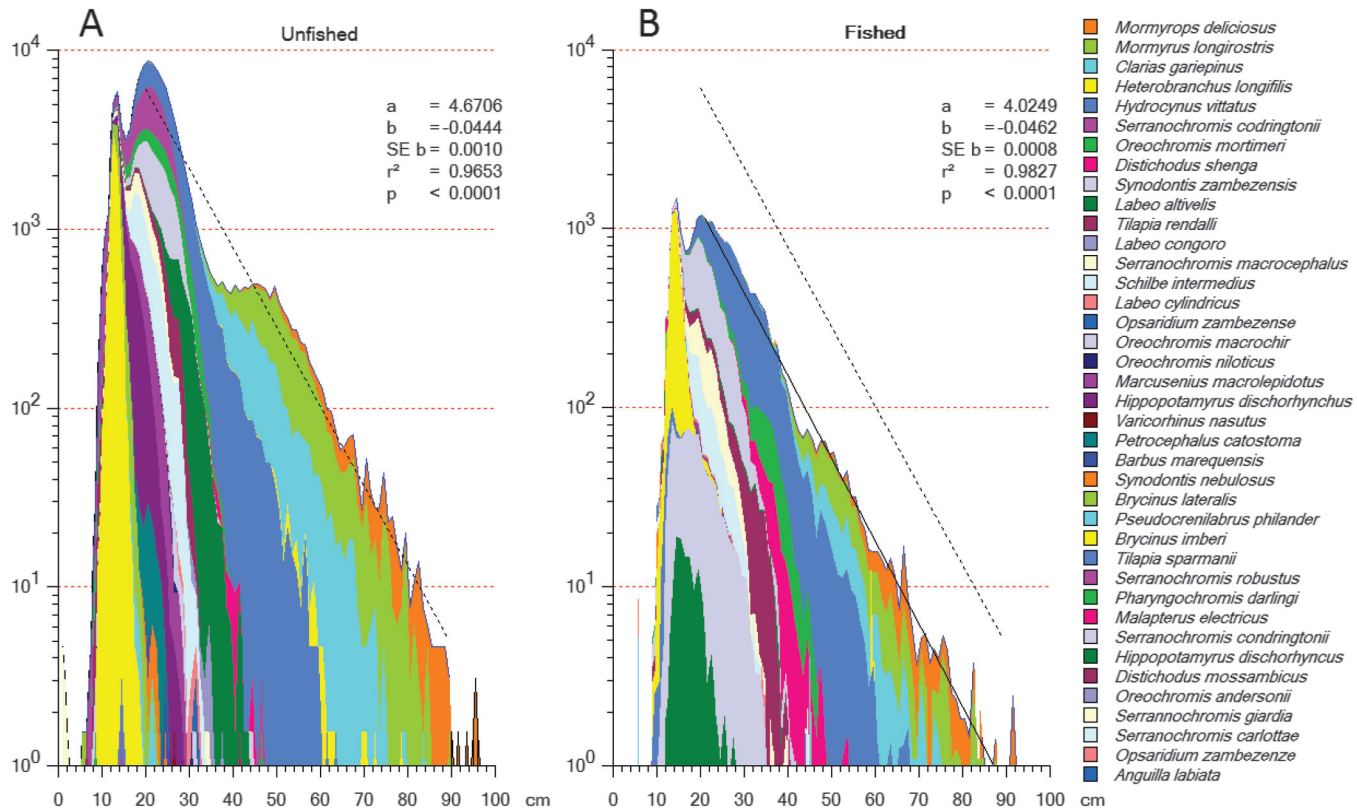
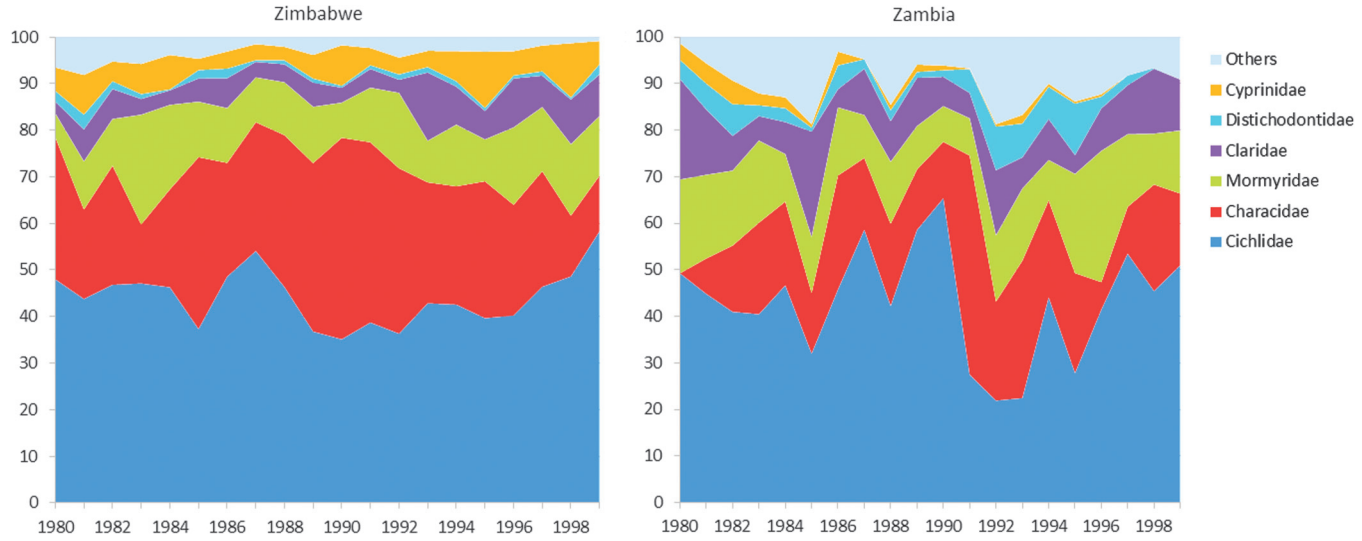


Fig. 4. The observed size spectra (standardized number of fish caught) by species in Lake Kariba from demersal experimental gillnet surveys 1980–1994: (A) unfished area, Zimbabwe; (B) heavily fished Zambian fishing grounds (ref. Fig. 1 for locations). Different intercepts with no significant difference between the slopes (regression lines) of the unfished (dashed lines) and the fished (continuous lines) communities indicate a significantly lower standing biomass but almost equal species (relative to the natural limnological gradient) and size compositions in the fished area. Modified from Kolding et al. (2003*a*) and Kolding and van Zwieten (2014). (Available in colour online.)



with individual weight (eq. M2) and the available prey (eq. M3). Encountered prey is consumed with a functional response that sets the feeding level of an individual (eqs. M4–M5), which is a dimensionless number between 0 and 1 and a measure of satiation. Consumed food is channeled into growth (eq. M6), and if the individual is mature (eq. M7), energy is used for reproduction (eq. M8–M9). To maintain coexistence of all asymptotic size groups, recruitment is limited by a Beverton–Holt stock–recruitment relationship (eq. M10). The consumption of the larger individuals is translated into corresponding predation mortality on the smaller individuals (eq. M12) such that there is a mass balance between consumption (and thus growth) and mortality. Additionally, all species are subject to a constant background mortality (eq. M12) and fishing mortality (eq. M13). Prey for the smallest individuals are accounted for by a resource spectrum of plankton with semi-chemostatic growth (eqs. M14–M15). The individual-level processes are scaled up to the community level by means of the McKendric–von Foerster equation (eq. M16).

Fig. 5. Relative catch composition (percent weight) in the inshore fishery between 1980 to 1999 by major families in Zimbabwe and Zambia based on catch assessment surveys (CAS). Modified from Kolding et al. (2003*a*). (Available in colour online.)



The model is calibrated to Lake Kariba by (*i*) adjusting the carrying capacity of the resource (κ) such that the simulated yields are in the correct range and (*ii*) correcting the maximum uptake rate (h, eq. M4) to fit the growth rates in the model to observed growth trajectories in the lake (Kolding et al. 1992; Fig. 6). This calibration causes all fish of the same weight class to have equal growth and mortality and thus does not distinguish between slow- and fast-growing varieties, but as Fig. 6 shows, the estimated growth of the actual species in Lake Kariba does not diverge much relative to size. The model consists of 19 different "asymptotic size groups", so that the community consists of a "species" within each group with asymptotic sizes ranging from 12 g to 10 kg. Fishing is composed of a large number of gillnets with different mesh sizes (Fig. 3), each with their own bell-shaped size-selection curves (Appendix A, Fig. A1); therefore, fishing is only selecting for size, not for species. The fishing patterns used in the simulations are estimated by using the observed mesh size distribution from Zambia and Zimbabwe (Fig. 3). A fitted log-normal curve represents the selectivity of each mesh size (see Appendix A). To move from individual mesh size selectivity to the total fishing pattern, the selectivity for each mesh size is weighed by the number of corresponding nets and summed (Appendix A, Fig. A3). The total selection pattern by weight is modeled by estimating the parameters w_m (maximum retention weight) and σ_m (standard deviation) in eq. M13 for Zambia and Zimbabwe, respectively, by converting length (L, in cm) (Appendix A, Fig. A3) to weight (w, in g) from the standard length–weight relationship $w = aL^3$, where a = 0.01. Both selectivity patterns have a hard cutoff, w_F, at 10 and 50 g for Zambia and Zimbabwe, respectively, to avoid catch of unreasonably small fish.

Results

The slopes of the modelled size spectra (from ≈20 to 100 cm) are similar to both the unfished (Lakeside) and the fished (Zambia) experimental sampling stations (Fig. 7A). The main difference between the fished and the unfished areas is that the density of fish by number is approximately 5 times lower in the Zambian area. The size spectra from the community model show a remarkably good fit with the observed size spectra in the catch curves of the experimental nets (Fig. 7A), even though the model has been calibrated with only a few parameters (Table 2). The resemblance between observations and simulations is limited to fish larger than ≈25 cm, which largely corresponds with the size at which the observed data are under-represented due to gear selectivity (Appendix A, Figs. A1, A2). The fished Zambian size spectrum is obtained by applying the modeled fishing pattern (Fig. 7B; Appendix A, Fig. A3) corresponding with the number of mesh sizes observed in Zambia (Fig. 3). The Zimbabwean selection pattern is regulated towards highest retention at larger sizes (Figs. 3 and 7B).

Figure 8 shows the total yields from the Zambian and Zimbabwean sides under increased effort using the fishing patterns from Fig. 7B. The fishing effort used to simulate the observed spectrum in Fig. 7A indicates that the Zambian fishery was still not fully exploited under the observed fishing pattern (mesh sizes and number of nets). Because the Zimbabwean side yielded five times less (about 1200 t·year^{-1}) on average, we can deduce from the model that this fishery was only lightly exploited in relation to the maximum potential yield at the time of the observations. We also see that the fishing effort must be approximately 5.5 times higher in Zambia to get a yield that is 5 times higher (Fig. 9). The number of fishers in Zambia was on average three times higher than in Zimbabwe, but they had about seven times more nets (Kolding et al 2003*a*).

To evaluate the impact of fishing on the fish community structure, we use the size spectrum slope, calculated for fish between 10 and 7000 g. A low change in slope indicates little impact on the relative size structure on the community. We find that the Zambian fishery is not changing the slope significantly more than the Zimbabwean fishery (Fig. 10), even though the yield is much higher. The observed slope in the experimental catches from Zambia is also not significantly different from the unfished area in Zimbabwe (Figs. 4 and 7A). However, we also find that the yield extracted from the Zambian side is closer to a point, where yield stops increasing and the slope steepens if effort expands without changing the fishing pattern. Moving beyond this point without decreasing the mesh sizes further means that large fish in the system are fished out relatively faster than the small fish and that the community structure will change towards a less desirable state from an ecosystem approach or diversity point of view. Nevertheless, given the particular fishing patterns of the two fisheries, the point at which the slope deteriorates is reached at a much lower effort and yield in the selective fishery in Zimbabwe compared with the less selective fishery in Zambia.

Discussion

With a conceptually relatively simple size-based model, we are able to closely reproduce the observed fished and unfished community structures in Lake Kariba and thereby explain how the less

Table 1. Model equations.

Encounter and consumption		
Prey size selection (–)	$\phi\left(\frac{w}{w_{prey}}\right) = \exp\left[-\left(\ln\left(\frac{w}{\beta w_{prey}}\right)\right)^2 \Big/ (2\sigma^2)\right]$	M1
Volumetric search rate	$V(w) = \gamma w q$	M2
Encountered food (g· year^{-1})	$E(w) = V(w) \int_0^{\max(W_\infty)} w_{prey}\phi\left(\frac{w}{w_{prey}}\right)\left(\sum N_i(w_{prey}) + N_r(w_{prey})\right)\mathrm{d}w_{prey}$	M3
Maximum consumption rate	$I_{max} = hw^n$	M4
Feeding level (–)	$f(w) = \frac{E(w)}{E(w) + I_{max}}$	M5
Growth and reproduction		
Somatic growth (g·year^{-1})	$g_i(w, W_{\infty,i}) = (af(w)hw^n - kw^p)(1 - \psi(w, W_{\infty,i}))$	M6
Maturity ogive (–)	$\psi_i(w, W_{\infty,i}) = \left[1 + \left(\frac{w}{\eta W_{\infty,i}}\right)^{-10}\right]^{-1}\left(\frac{w}{W_{\infty,i}}\right)^{1-n}$	M7
Recruitment		
Egg production (eggs·year^{-1})	$R_p(W_{\infty,i}) = \frac{\epsilon}{2w_0}\int_{w_0}^{W_{\infty,i}} (\alpha f(w)hw^n - kw^p)\,\psi(w, W_{\infty,i})N_i\mathrm{d}w$	M8
Maximum recruitment (eggs·year^{-1})	$R_{max}(W_{\infty,i}) = K\kappa_r(\alpha f_0 hw_0^n - kw_0^p)W_{\infty,i}^{2n-q-3+a}\Delta W_{\infty,i}$	M9
Recruitment (eggs·year^{-1})	$R(W_{\infty,i}) = R_{max}(W_{\infty,i})\frac{R_p(W_{\infty,i})}{R_p(W_{\infty,i}) + R_{max}(W_{\infty,i})}$	M10
Mortality		
Predation mortality (year^{-1})	$\mu_p(w_{prey}) = \sum_i \int_{w_0}^{\infty} \phi\left(\frac{w}{w_{prey}}\right)(1 - f(w))V(w)N_i(w)\mathrm{d}w$	M11
Background mortality (year^{-1})	$\mu_{b,i} = \mu_0 W_{\infty,i}^{n-1}$	M12
Fishing mortality (year^{-1})	$F = F_0 \exp\left(\frac{-\ln\left(\frac{w}{w_m}\right)^2}{2\sigma_m}\right)$	M13
Resource spectrum		
Resource dynamics (g·year^{-1})	$\frac{\partial N_r(w)}{\partial t} = r_0 w^{n-1}(\kappa(w) - N_r(w)) - \mu_p(w)N_r(w)$	M14
Carrying capacity (g$^{\lambda-1}$)	$\kappa(w) = \kappa_r^{-2-q+n}$ for $w < w_{cut}$	M15
Conservation equation	$\frac{\partial N(w, W_{\infty,i})}{\partial t} + \frac{\partial g_{i(w)}N(w, W_{\infty,i})}{\partial w} = -\mu_p(w)N(w, W_{\infty,i})$	M16

Note: Units are in parentheses; dash indicates dimensionless unit.

selective fishery in Zambia is able to provide higher yield than the more selective fishery in Zimbabwe, while still conserving the relative community structure. The main points that emerge from the model and are validated by the observations are that focusing the fishing pattern under high effort on predominantly small individuals produces little impact on the community and the largest maximum yield, whereas at low effort, the highest individual catch rates are obtained by focusing on larger individuals. These findings are important, as the development of the uncontrolled fishery on the Zambian side of Lake Kariba with increasing effort, decreasing catch rates, and subsequently decreasing mesh sizes to compensate for decreasing returns is conventionally interpreted as emergent signs of overfishing. Despite producing a higher yield while conserving relative community structure, the less selective fishery in Zambia is conforming to conventional indicators of destructive and unsustainable fishing patterns such as increased use of illegal small-meshed gears, strongly reduced stock abundance, and decreased mean size of fish in catches (Tweddle et al. 2015).

The paradox, however, as shown both by the empirical observations and theoretical results here, is that the uncontrolled open-access fishery on the Zambian side of Lake Kariba appears to attain the desired goals set in international agreements. By ignoring the minimum mesh size regulations, the Zambian fishery produces the highest sustainable yield (UNCLOS 1982) while maintaining the relative fish community structure (CBD 1992). These positive counterintuitive results of noncompliance are created by a rational individual response to the open-access regime. When effort grows and catch per unit effort decreases, it is a logical and necessary reaction of individual fishers to gradually decrease their mesh sizes to maintain an acceptable catch rate, albeit the result is increasing amounts of small fish over a larger species diversity as an increasing number of small species enter the fishery (Kolding et al. 2015*a*). Thus, the increased effort is distributed over a wider range of the fish community so that catch rates are maintained with limited change to the overall size structure of the community (Fig. 10). This, so-called "fishing down process" (Welcomme 1999) is generally considered as a sign of a deteriorating and harmful situation (Pauly et al. 1998; Tweddle et al. 2015), with the added problem that an increasing number of fishing methods become technically illegal as they target smaller and

Table 2. Parameters used in the size-based model.

Encounter and growth		Value	Unit
α	Assimilation efficiency[a]	0.6	—
n	Exponent of maximum consumption[b]	0.75	—
h	Factor of maximum consumption[c]	28*	g^{1-n}·$year^{-1}$
q	Exponent of search volume[d]	0.75	—
p	Exponent of standard metabolism[e]	0.75	—
k	Factor of standard metabolism[f]	2.4	g^{1-n}·$year^{-1}$
γ	Factor for volumetric search rate[g]	5×10^{-9}	g^{-q}·$year^{-1}$
β	Preferred predator–prey mass ratio[h]	100	—
σ	Width of size-selection function[i]	1.3	—
η	Size at maturation relative to asymptotic size[j]	0.25	—
f_0	Expected feeding level[k]	0.6	—
K	Maximum recruitment factor[l]	1×10^{4}	—
Mortality			
μ_0	Factor for background mortality[m]	3	g^{1-n}·$year^{-1}$
a	Physiological mortality[n]	0.58	—
Resource spectrum			
r_0	Productivity of resource spectrum[o]	4	g^{1-p}·$year^{-1}$
κ_r	Carrying capacity of resource spectrum	3.3×10^{9}*	$g^{\lambda-1}$
w_{cut}	Cutoff size of resource spectrum	1	g
Fishing mortality			
F_0	Level of effort	Free	$year^{-1}$
w_F	Smallest size caught	Free	g

Note: An asterisk (*) means that the parameter is specifically calibrated to Lake Kariba.

[a]Kitchell et al. (1977).

[b]Jobling (Brown et al. 2004) states that $2/3 < n < 3/4$. We have used $n = 3/4$ to be consistent with von Bertalanffy growth curves.

[c]Adjusted such that emergent growth rates are in the range of those observed.

[d]Considerations on the bioenergetic budget of swimming predict a value of q between 2/3 and 1 (Andersen and Beyer 2006).

[e]West et al. (1997).

[f]The data of Winberg (1956) indicate a standard (resting) metabolism factor for fish of about 4 $g^{0.25}$·$year^{-1}$ at 10 °C.

[g]Calculated from the other parameters as specified in Andersen and Pedersen (2010).

[h]Ursin (1973) and Jennings et al. (2001).

[i]Ursin (1973) finds $\sigma \approx 1$ for a single species. To account for species diversity within trait class classes, this has been increased to $\sigma = 1.3$.

[j]Beverton (1992).

[k]Andersen and Pedersen (2009).

[l]Determines the relation between piscivory and zooplanktivory in early life stages (Houle et al. 2013).

[m]Adjusted to lead to a background mortality of the same order (but lower) than the predation mortality.

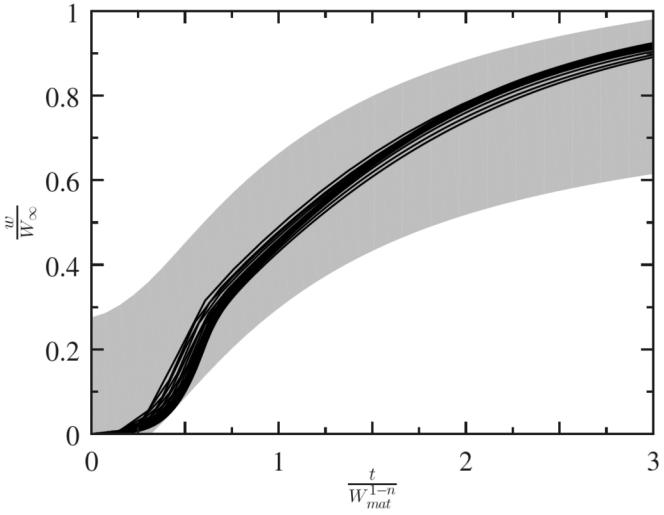
[n]The physiological mortality describes the relative strength of predation; for derivation, see Andersen and Beyer (2006).

[o]Hartvig et al. (2011).

smaller fish (Kolding et al. 2015*a*). Our results, however, indicate a need to reconsider this traditional evaluation.

In African inland fisheries, food is the major objective and small fish often have the same price per unit weight as large ones (Brummett 2000), confirming the high demand. Small fish, either juveniles or species, have higher productivity per unit biomass than large fish and are generally lower in the trophic chain (Lorenzen 1996; Jennings et al. 2001; Brown et al. 2004). In many fishes studied, the somatic growth of adults contributes less than one-third and seldom more than half to the total production (Morgan et al. 1980). In terms of food production, this means that harvesting small fish and juveniles is most efficient as energy is lost in metabolic costs when targeting large fish at higher trophic levels. Furthermore, the Zambian fishing pattern does not impair sustainability in terms of renewed recruitment of large slow-growing species. In Lake Kariba, as in most other African inland fisheries, the predominant gear is gillnets with a bell-shaped selectivity curve (eq. M13). Thus a decrease in mesh sizes will not

Fig. 6. Averaged estimated von Bertalanffy growth curves from 22 fish species in Lake Kariba (Kolding et al. 1992) ±1 SD (gray area) and the emergent growth of 19 species in the size-based model (black lines). The *y* axis is scaled by the asymptotic weight and the *x* axis is time scaled by W_{mat}^{1-n}, which is proportional to age at maturity.



affect the adults with a relatively large maximum size, the so-called BOFFFs (big old fat fecund females; Hixon et al. 2014), as more of these will escape being caught (Fig. 7B), securing continued reproduction. Adjusting the fishing mortality according to productivity and thereby shifting the fishing mortality towards small fish as the Zambian fishers do by decreasing the average mesh sizes (Fig. 3) is in accordance with the "balanced harvest" principle suggested by Garcia et al. (2012) to mitigate the adverse effects of fishing on community structure and address food security.

Although there is increasing evidence of the demographic, structural, and genetic effects of selective fishing on adults, resulting in age truncations, species loss, increased instability, and possible induced evolutionary effects (Rice and Gislason 1996; Andersen and Brander 2009; Jørgensen et al. 2007), there are very few known examples of balanced fishing across species and sizes. Nearly all comprehensive observations on fished communities come from managed fisheries, and these all have strong elements of size-selective restrictions. In fact, for fisheries with limited information and lack of regular stock assessments, the cheapest and easiest option for managers is to regulate the fishing pattern through gear or size limitations (Misund et al. 2002; Kolding et al. 2014). Examples of less selective fishing therefore have to be found among fisheries in which limited or no enforcement of formal regulations exists. Among the latter are many small-scale fisheries in developing countries that lack the resources for effective compliance. In the few cases in which selectivity has been studied in such fisheries, the results show that the rapidly adapting multigear, multispecies artisanal fisheries often seem to be producing an overall species, abundance, and size composition in their catches that closely matches the ambient ecosystem structure (Misund et al. 2002; Jul-Larsen et al. 2003; van Zwieten et al. 2011; Kolding and van Zwieten 2014).

Harvesting natural ecosystems will inevitably make an impact on abundance and selective exploitation on targeted species, and sizes will change the community structure and composition. The international agreements to keep fish communities at the levels of maximum sustainable yields (UNCLOS 1982; WSSD 2002) while making the least structural and functional disturbances to the ecosystem (UNEP 2000) are therefore difficult objectives to reconcile (Hilborn 2007; Law et al. 2015; Kolding et al. 2015*b*). The fishing

Fig. 7. (A) The observed size spectra (standardised number of fish caught) from the 1980–1994 experimental gillnet surveys in Lake Kariba from the unfished (dotted black line) Lakeside area in Zimbabwe and the fished (dotted gray line) area in Zambia (Fig. 4) and the modeled unfished (solid black line) and fished (solid gray line) size spectra (scaled with a constant factor c to get comparable units with observations). Fish below ≈25 cm in the observed size spectra are not well sampled due to gear selectivity (see Appendix A). There is no significant difference in the descending slopes between the fished and unfished distributions (Kolding et al. 2003*a*). (B) Modeled fishing selectivity pattern in Zambia (solid black line) and in Zimbabwe (dashed gray line). The Zambian fishing pattern was used to generate the fished size spectrum in part A.

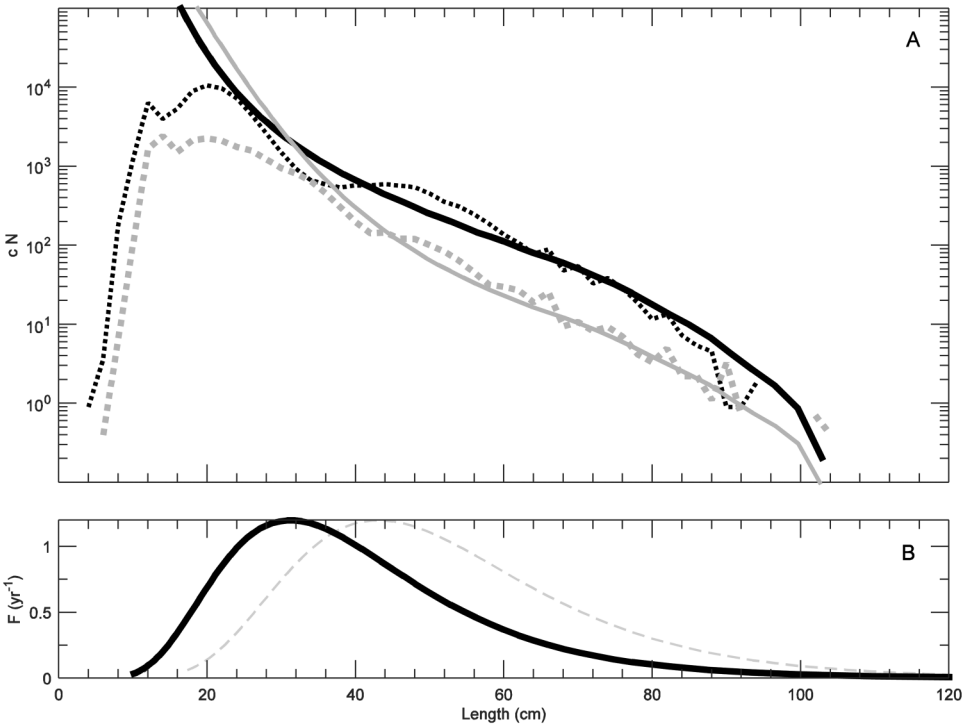


Fig. 8. Yield from the less selective fishery on the Zambian side (black line) and the selective fishery on the Zimbabwean side (gray line) as a function of effort (F_0) using the fishing patterns in Fig. 5. Dotted lines are the expected F_0 corresponding to the observed ≈6000 t·year^{-1} in Zambia and ≈1200 t·year^{-1} in Zimbabwe.

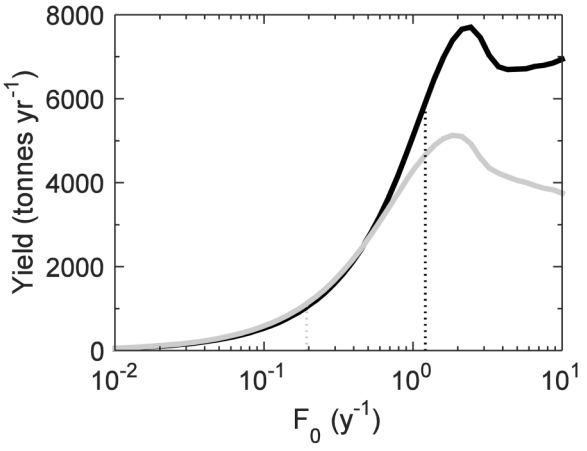
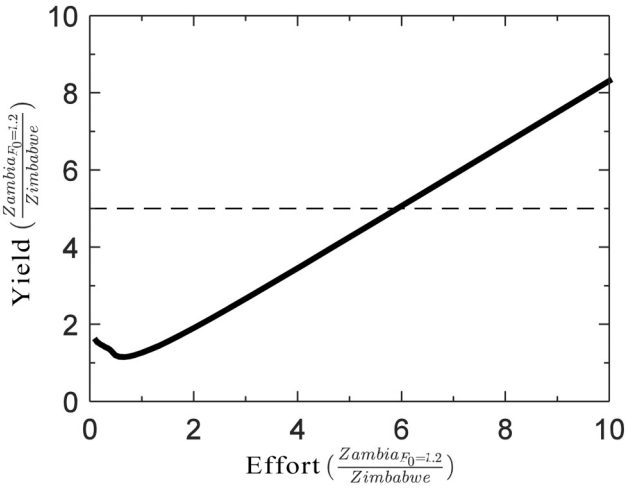


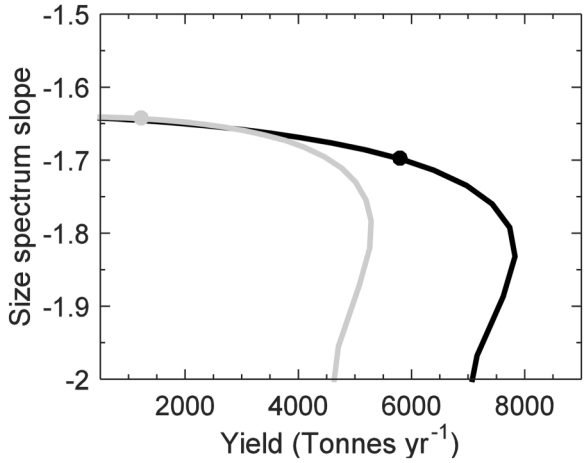
Fig. 9. The difference in yield between Zambia and Zimbabwe as a function of relative effort. The yield and effort from Zambia are held constant with F_0 = 1, corresponding to the effort level used to model the Zambian fished spectrum in Fig. 5A. To obtain a fivefold higher yield in Zambia than Zimbabwe, the relative effort is ≈5.5 times higher.



mortality on a population is shaped by a combination of "how" we fish (fishing pattern) and "how much" we fish (fishing pressure), but often the distinction between these two separate factors are ignored and the effects become merged (Kolding and van Zwieten 2011, 2014). The minimum size regulations imposed in Lake Kariba are typical for a large number of industrial and small-scale fisheries, but as this study shows, such regulations are difficult to implement unless enforced when the market has no particular size preferences. The inherent tendency for many small-scale fishers to violate size-based regulations has an economic basis and the resulting universal conflict between managers and fishers over size regulations is therefore largely futile and rarely has ecological justification (Kolding and van Zwieten 2011).

Our results call for a re-evaluation of the size-based management regulations that are ubiquitous in most fisheries if the

Fig. 10. The size spectrum slopes from Zambia (black line) and Zimbabwe (gray line) under increasing yield and given the different size selection pattern from each fishery (Figs. 3 and 5). The black and the gray dots represent the average observed yields from Zambia and Zimbabwe, respectively. Yield can increase up to a maximum achievable with only small changes in slopes, after which increased effort will mainly affect slope without gain in yield. Thus, using a less selective fishing pattern as in Zambia gives significantly higher yields with only small changes in the slope.



Convention on Biological Diversity principle of maintaining ecosystem structure is to be taken seriously. In contrast to conventional expectations from standard fisheries theory, the unregulated fishing pattern that has evolved on the Zambian side of Lake Kariba seems to fulfill most of our goals: it is high yielding and community structure conserving and sustains the livelihood of many fishers. The negative sides are that the standing biomass in the fished areas is typically low, with corresponding low individual catch rates and, consequently, low individual revenue (Burgess et al. 2015). The negative aspects, however, are more a question of fishing effort ("how much" fishing) than of size regulations ("how" to fish). If regulations are needed, it would therefore be better to control access than to regulate the fishing pattern. Fisheries management is always a balance of trade-offs (Link 2010; Andersen et al. 2014), and for many fisheries, particularly in the Northern Hemisphere, the value of the catch is strongly correlated with the size of the fish, in which case, size restrictions combined with low effort may be appropriate. In the developing world, however, food production, in particular healthy food containing essential micronutrients, is still of major importance (Food and Agriculture Organization of the United Nations (FAO) 2014; High Level Panel of Experts on Food Security and Nutrition (HLPE) 2014), and in such situations, a fishing pattern such as the Zambian side of Lake Kariba seems to be optimal from ecological, sociopolitical, and nutritional aspects (Kolding et al. 2015*a*), the latter because small fish are usually sundried and eaten whole, in contrast to large fish, which are filleted or smoked, thereby losing many essential micronutrients (Longley et al. 2014) in addition to being more expensive to process. We hope that this study will inspire more research into how local communities develop fishing patterns and how these affect the fish community on which they depend.

Acknowledgements

The fishery data used in this study were collected by the Lake Kariba Fisheries Research Institute (Zimbabwe) and by the Lake Kariba Research Unit and the Sinazongwe Fisheries Training Center (Zambia). Much of the empirical data compilation and background analyses were performed during the Zambia/Zimbawe SADC Fisheries project, sponsored by Norad (Norway) and Danida (Denmark) and a four-year research project on freshwater fisheries development in the SADC area (Management, co-management or no management? Major dilemmas in southern African freshwater fisheries) funded by the Norwegian Research Council. We are indebted to all of these institutions for help and assistance. NSJ and KHA were supported by the Centre for Ocean Life, a VKR Centre of Excellence supported by the Villum Foundation.

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Appendix A starts on the next page.

Appendix A. Fisheries selectivity patterns in Lake Kariba

1. Estimated selectivity in experimental nets

Fig. A1. Estimated log-normal selectivity curves on the experimental gillnet catches on the Zimbawean side of Lake Kariba (1980–1994) from mesh sizes 38 mm to 178 mm and the combined estimated selectivity (thick black line). Estimation done in Pasgear II (Kolding and Skålevik 2011) using the SELECT method (Millar and Holt 1997). (Available in colour online.)

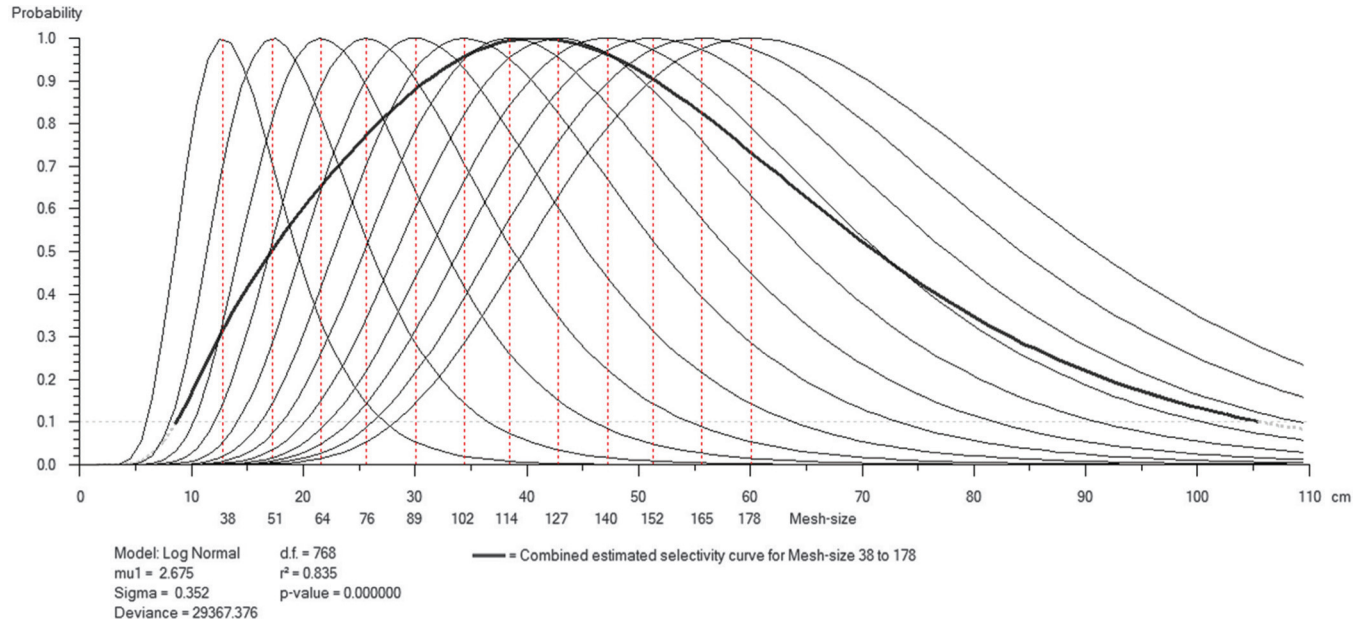


Fig. A2. The observed (gray bars) and corrected for selectivity (open bars) catches (relative frequencies by 1 cm intervals) in the experimental gillnets catches on the Zambian side of Lake Kariba (1980–1994) from mesh sizes 50 mm to 152 mm. Superimposed (black line) is the estimated overall log-normal selectivity curve. Catches of small fish are underrepresented relative to abundance due to selective catchability from less than around 20 cm TL.

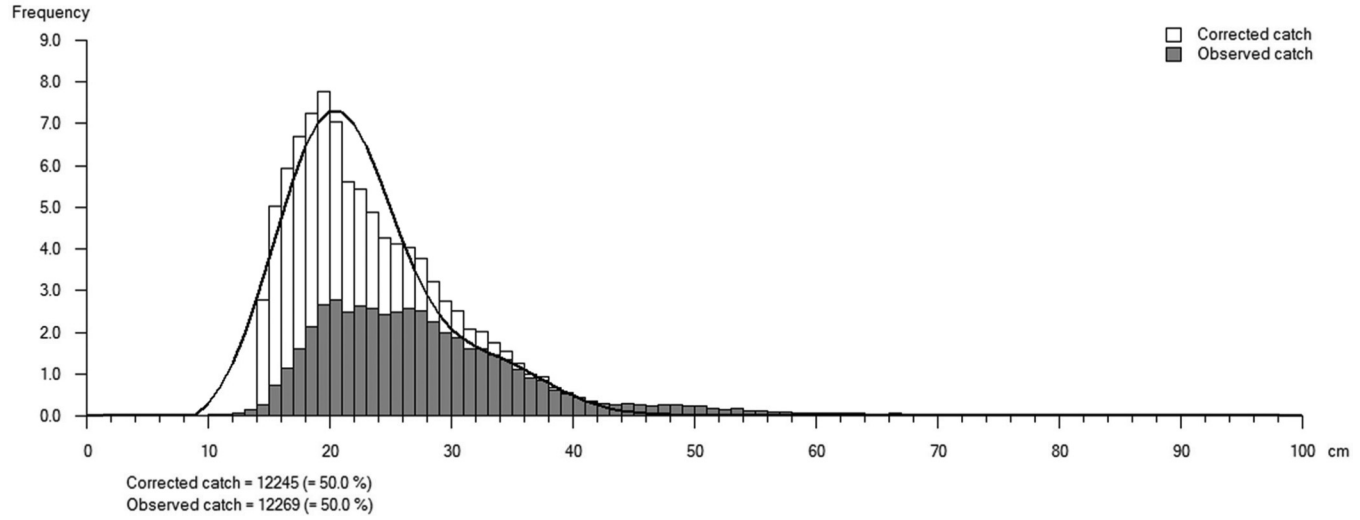
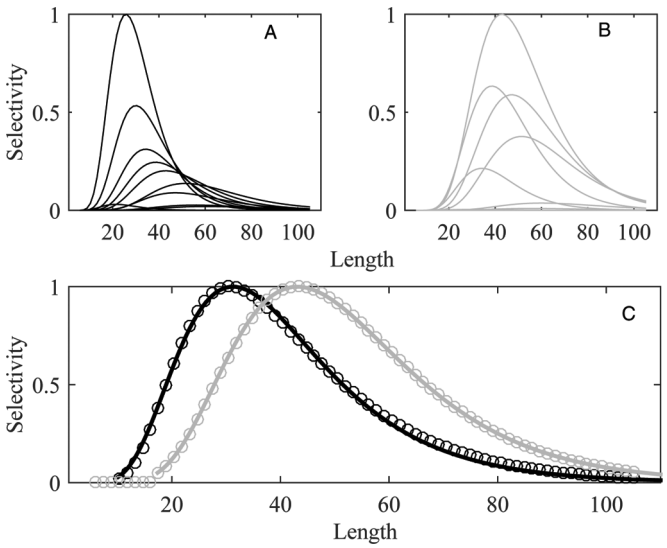


Fig. A3. The overall selectivity of artisanal gillnets in (A) Zambia and (B) Zimbabwe (spread and length parameters from Fig. A1, height from each mesh size from Fig. 3, main text). (C) The sum of length-specific gillnet selectivities gives the total selectivity, or fishing pattern, for Zambia (black circles) and Zimbabwe (gray circles). The solid line is the modeled selectivity (eq. M13) in Zambia (black) and Zimbabwe (gray).



2. Calculated selectivity in the artisanal fishery

The calculated selectivity patterns in Lake Kariba are based on the predominant fishing gear: a gillnet with a log-normal bell-shaped selectivity (Fig. A1). The individual mesh selectivity functions are formulated as (Millar and Holt 1997)

$$\text{(A1)}\qquad \frac{1}{L}\exp\left[\mu_1 + \log\left(\frac{m_i}{m_1}\right) - \frac{\sigma^2}{2} - \frac{\left(\log(L) - \mu_1 - \log\left(\frac{m_i}{m_1}\right)\right)^2}{2\sigma^2}\right]$$

where L is fish length, μ_1 is a constant estimated by the SELECT method, m_1 the smallest mesh size in the series, m_i is mesh size i, and σ is the spread. Parameters used are estimated in Fig. A1. To obtain the total selection pattern, the relative heights of the individual curves are adjusted by the number of observed nets of each mesh size and summed for Zambia and Zimbabwe (Fig. A3).

References

Kolding, J., and Skålevik, Å. 2011. PasGear II. A database package for experimental or artisanal fishery data. University of Bergen, Norway. Available from http://www.imr.no/forskning/bistandsarbeid/nansis/pasgear_2/en [accessed 10 January 2015].

Millar, R.B., and Holst, R. 1997. Estimation of gillnet and hook selectivity using log-linear models. ICES J. Mar. Sci. **54**: 471–477. doi:10.1006/jmsc.1996.0196.